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AN EQUITABLE MARRIAGE: A FOCAL STUDY OF A BARN SWALLOW (*HIRUNDO RUSTICA*) NEST ON LUNDY

by

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ABSTRACT

Adult attendance at a single barn swallow (*Hirundo rustica*) nest was observed and recorded during July 2010 from when the chicks were between six and eight days old. The visits to the nest made by the male and female adults were equal in their duration, rate-per-minute and number, and were close to chance in their sequencing. There was a marginal decline in these visits over a seven-day period. Equality of parental investment is discussed in the context of the reproductive strategies of swallows and future directions for research on the nesting swallows of Lundy are suggested.

Keywords: *barn swallows, nest visits, reproductive strategy*

INTRODUCTION

Barn swallows (*Hirundo rustica*) are both a socially monogamous and sexually dimorphic species. Whilst they mate monogamously both males and females will engage in extra-pair copulations, leading to extra pair paternity (EPP). Turner (Turner, 2006) has summarized a number of studies investigating EPP and her results are presented in Table 1.

Table 1: A summary of six studies showing percentage of chicks not fathered by the female's social mate and the percentage of broods with at least one extra-pair chick.

Adapted from Turner (2006: 87)

| Percentage chicks that are extra-pair | Percentage broods with extra-pair chicks | Number of chicks/broods | Locality of study |
|---------------------------------------|--|-------------------------|-------------------|
| 29 | 45 | 45/11 | Ontario, Canada |
| 31 | 50 | 391/86 | Ontario, Canada |
| 23 | 49 | 306/61 | New York, USA |
| 28 | 33 | 261/63 | Denmark |
| 29 | 52 | 214/52 | Italy |
| 18 | 32 | 674/170 | Spain |

Table 1 demonstrates that EPP can be a significant contributor to reproductive output, with a minimum of a third of all broods in the summarized studies containing at least one extra-pair chick.

Engaging in EPP is regarded as a fitness maximizing strategy and can be directly related to parental investment theory (Trivers, 1972). In a sexually reproducing species parental investment includes the donation of a gamete through to feeding and protection post-partum or, in the case of birds, after hatching. Female birds invest more at the gamete level, producing eggs that require more energy, nutrients and time to produce than sperm. Any investment that a parent makes in one offspring is an investment that cannot be made in another and we should expect natural selection to favour behavioural strategies that trade-off continued investment against possible future investments and yield. Given the differential costs at the level of gamete we should also anticipate sex differences in the tipping points for those trade-offs. To this end, male parental behaviour varies from simply the donation of sperm, with no post copulation investment in the offspring (nor the mother) through to extensive paternal care. Females cannot achieve reproduction as cheaply as some males.

EPP amounts to a gamete donation outside the context of a socially monogamous pair bond. Social monogamy represents parental investment beyond gamete donation for both male and female, but not necessarily equality of investment. A male bird may invest in a monogamous bond and take a share of the parental duties but also divert time and energy to finding and securing extra-pair mating opportunities. The more resource spent in pursuit of EPP, the less that can be spent on paternal duties at the nest. The fitness benefits of this behaviour are obvious, the male increasing the likely amount of genetic representation in the next generation. Any extra-pair chicks will be raised for free, making EPP a relatively cheap investment. Meanwhile, the mother in the pair-bond will have a significant investment in any eggs produced and may well exert significant effort to keep them alive, which can only benefit the father (Trivers, 1972). To this end EPP can be seen as a form of bet-hedging strategy for the male, where any parental investment from the cuckolded male cannot be guaranteed (see below), but some maternal investment is likely thereby increasing the overall reproductive success.

EPP brings advantages for females also. More than one father for a brood introduces genetic variation that in turn may increase the likelihood of some chicks surviving to reproductive age. The sexual dimorphism of swallows is indicative of female choice, and a huge amount of work has investigated this, focusing mainly upon tail length, but also spot size on tail feathers and general feather condition (Turner, 2006). Tail length is a possible indicator of underlying male qualities of robustness, such as immunocompetence and parasite resistance (Kose & Møller, 1999; Møller et al., 1998; Saino, Bolzern, & Møller, 1997; Saino & Møller, 1996). If these traits are heritable it is possible that female choice is indirectly selecting for them, as they would clearly benefit any offspring. Therefore, males with high value, sexually selected traits, such as long tails would be more likely to secure extra-pair copulations than those with lower value traits (Møller & Tegelström, 1997). Those with lower value traits should be more likely to offer paternal investment. However, males should differentially adjust their paternal investment in line with the risk of EPP, thereby offsetting the costs of investing in an unrelated chick (Møller, 1988). Thus in areas where EPP risk is high, paternal investment should be less than maternal investment at the nest. This will be reflected by relatively reduced nest attendance and feeding of chicks, as well as mate guarding strategies to prevent cuckoldry in the first instance (Turner, 2006).

Colony structure can impact upon the likelihood of EPP by providing opportunity for undetected extra pair activity (Ramos et al., 2014) and is more likely to occur when swallows are nesting in dense colonies (Turner, 2006). Colony structure may therefore provide a cue to the likelihood of EPP that defensive males can use. In a low density nesting situation EPP should be low to non-existent, and consequently paternal investment should be close to equality with female investment at the nest.

From personal observation, the breeding swallows on Lundy represent a low-density colony structure with a few nests scattered throughout the village even during the most successful breeding years. Lundy presents an ideal habitat for barn swallows, providing open ground with livestock and some still water sources that support insects, and these are close to the village, which in turn provides nesting opportunities. Barn swallows generally forage close to their nests, within about 500 metres (Turner, 2006), and they are not territorial foragers. Given this the Lundy swallows may be limited to the more southerly parts of the island where they must forage together. Weather conditions on the island may well cause shifts in insect availability and aerial conditions for hunting throughout the breeding season, but sheltered hunting should be available. For example, strong westerly winds from the Atlantic should promote hunting along the east coast. Overall prey abundance and distribution throughout the breeding season may well cap the size of the breeding population for the swallows. The phenology of prey across the summer should also predict when breeding begins and how many broods might be attempted (Lack, 1950).

The study reported in this paper represents an initial investigation into the breeding swallows on Lundy, conducted during a university animal behaviour field trip in 2010. A focal nest was chosen in the village and filmed over a two-week period in order to record nest attendance behaviour by the adults during one brood and to gain a good sample of this behaviour. Given the low density nesting on the island the main hypothesis was that parental investment would be at equality. The nature of the nesting should have reduced the opportunities for extra-pair copulation such that males would be less likely to engage in EPP and also more likely to invest in nest visits and feeds. Changes in investment over time, time of day effects and sequences in adult visiting behaviour were also analysed.

METHODS

Nest location

The nest was located above the main ground floor entrance of Old House North, at the intersection of the porch ceiling and wall. Access to Old House North is across a courtyard, bounded by walls and buildings. The main entrance is north facing and secluded within a large porch with an arched south facing entrance directly to the west of and in line with the door. As a consequence of this position the north-facing nest was shaded and only low levels of ambient light were maintained throughout the day. The nest was also sheltered from the weather and predators. Guests staying at Old House North would walk directly under the nest on a regular but infrequent basis during the day, but the nest would be too high to reach without the aid of a ladder. Human presence was therefore unlikely to cause any particular difficulties for the swallows.

Chicks

The nest contained four chicks attended by an adult male and female. The chicks were not removed from the nest at any time and so their age was estimated using limited visual cues from film. At the time of the first recording (film 00153) the chicks appeared to be between 6 and 8 days old (Turner, 2006).

Camera and camera placement

A Sony digital camcorder was placed on a tripod in the farthest corner from the nest. At its full extension the tripod could not equal the elevation of the nest, and so the camera was angled upward providing shots from slightly below the nest. At this angle the parents were visible and sexing them was possible in the majority of visits. The camera was always attended by at least one student who would remain outside the porch in the courtyard for the majority of the time. On occasion the camera would require operation and students would also need to make notes for a separate study that they were conducting, so at least one person would enter the porch. To this end the swallows were aware of human presence. Given the choice of nest site it is unlikely that this presence would disturb the swallows.

Time of year and film sample

Filming was conducted between 18 and 31 July 2010. Recordings were made during daylight hours. 38 separate recordings were made, amounting to over 15 hours of footage. Some of this footage was not usable, due to the camera being moved out of alignment on its tripod or the zoom function being altered. From the remaining film a sample of 12 films were taken spanning the first seven days of recording, capturing nest activity that occurred well before fledging. This amounted to just under five hours of footage (c. 33% of the entire sample). The mean length of each film was 24.97 minutes. As can be seen from Figure 1 there was some skew in the distribution of film length, with the majority of films in the 25-minute or greater range. The 12 films covered times between 09:48 to 17:46 (see Table 2).

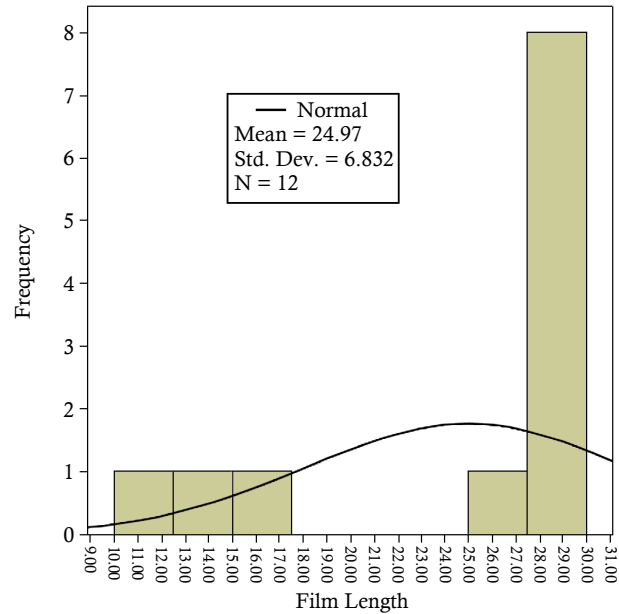


Figure 1: Frequency of film duration in minutes. The mean duration is 24.97, the median 28.79 and the mode 29.40. A normal distribution line has been fitted to highlight the skew of -1.261

Table 2: Film identity number, day of filming, time-of-day and duration of each subsample

| Film identity | Day | Start time | AM/PM | Duration (mins:secs) |
|---------------|-----|------------|-------|----------------------|
| 00153 | 1 | 17:17 | PM | 29:53 |
| 00154 | 2 | 15:24 | PM | 29:52 |
| 00155 | 3 | 11:15 | AM | 29:40 |
| 00156 | 3 | 13:31 | PM | 12:41 |
| 00157 | 3 | 16:56 | PM | 29:54 |
| 00158 | 4 | 14:15 | PM | 28:18 |
| 00159 | 5 | 13:35 | PM | 29:40 |
| 00160 | 6 | 11:03 | AM | 16:18 |
| 00172 | 6 | 14:41 | PM | 27:59 |
| 00174 | 6 | 15:35 | PM | 13:19 |
| 00175 | 7 | 09:48 | AM | 25:14 |
| 00176 | 7 | 10:22 | AM | 29:55 |

Behavioural categories and coding

All 12 films were coded using the Observer XT (version 11, Noldus) behavioural observation software on a Dell Latitude laptop. Coding was undertaken at Middlesex University. In order to establish categories the films were watched twice. Three categories for Sex were established: Male, Female and Unknown. Sexing was achieved by using tail length and markings. The Unknown category was used when sex could not be established due to camera angle or the position of the bird obscuring the feathers. This category enabled the calculation of total visits. Two mutually exclusive behavioural categories were coded under each Sex: Present and Absent. Present was recorded when an adult bird landed on the nest. Absent was recorded when an adult bird initiated leaving which was regarded as the first move away from the nest that resulted in flight: typically a head turn and shoulder drop. Both Present and Absent could be accurately ascertained by running and re-running the film forward and backward in slow motion. These were effectively start-stop categories. Observer recorded the frequency, rate per minute and duration of these behaviours. A reliability analysis was not conducted but the films were processed twice. In the first wave the films were coded in real time, using the slow motion and backward running facilities at each visit. In the second wave each parental visit for each film was located and then recoded. This amounted to a correction procedure enabling some Unknown birds to be sexed and a few original sex allocations to be altered.

Ethical note: The ethics committee of the School of Psychology, University of East London (for whom the author worked at the time) judged this work to be ethically sound. This was a purely observational study and the work was conducted according to the guidelines established by the Association for the Study of Animal Behaviour (<http://asab.nottingham.ac.uk/ethics/guidelines.php>).

RESULTS

All analyses were conducted using IBM SPSS version 21 unless otherwise stated.

Primary analyses

The principal aim was to establish whether or not both adults were at equality in terms of their investment at the nest. Investment was measured using the duration, rate per minute and number of visits. Visits were assumed to be feeds with occasional attendant nest maintenance such as the removal of faecal sacs. The following analyses will focus upon the behavioural category of Present, as this gives information about the time spent at the nest. The Absent variable will incorporate time spent foraging but also other behaviours necessary to the adults, behaviours that have not been tracked. Table 3 displays the descriptive statistics for Present by Sex, including for the Unknown category.

Table 3: Mean (and standard deviation) of the duration and rate per minute of the Present variable across all 12 films by Sex. Also the total number of visits across all 12 films as measured through the Present variable by Sex

| | Duration in seconds | Rate per minute | Number |
|----------------|---------------------|-----------------|--------|
| Male | 9.24 (8.82) | 0.34 (0.23) | 110 |
| Female | 16.12 (12.66) | 0.35 (0.21) | 106 |
| Unknown | 2.04 (3.12) | 0.07 (0.08) | 18 |

As can be seen from Table 3 the total number of visits for males and females is extremely close in value, and Unknown is a clear outlier. To this end Number was not entered as a variable into the following analyses, but the duration and rate-per-minute were treated as key investment variables that could differ between male and female adults.

A one-way analysis of variance (ANOVA) across duration and rate per minute was conducted using Sex as a grouping variable. This was found to be significant for both duration ($F=7.202$ (2,33) $p=0.003$) and rate per minute ($F=9.425$ (2,33) $p=0.001$). However, the Levene's Test for homogeneity of variance was also significant indicating that the data was not parametrically distributed. Given the low number of Unknown observations this group was removed and a two-tailed independent samples T-Test was conducted for the key behavioural variables across Male and Female. In this case the Levene's Test was not significant, indicating a parametric data set. The results for duration ($t=-1.545$, $df=22$, $p=0.137$) and rate per minute ($t=-0.132$, $df=22$, $p=0.896$) were both found to be non-significant.

To be sure of this data a two-tailed Runs test was conducted on the key behavioural categories collapsed across Sex. This test establishes whether or not the data is random. The results for duration ($N=-2.198$, $p=0.028$) and rate per minute ($N=-2.875$, $p=0.004$) were both significant indicating that the null hypothesis can be rejected and this data regarded as non-random. The raw data for all three behavioural variables, by Sex, is displayed in three bar charts in Figure 2.

In summary, male and female investments appear to be at equality across the subsample of films analysed.

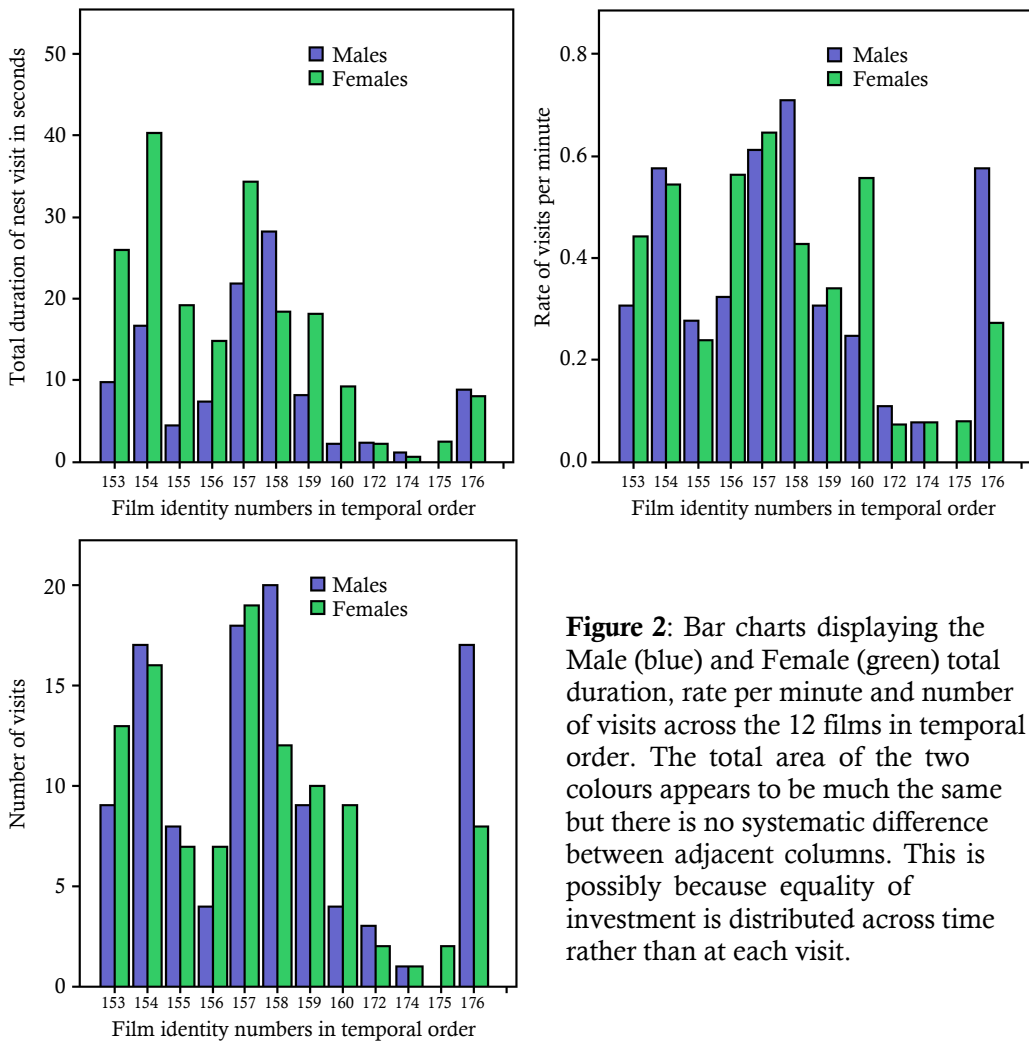


Figure 2: Bar charts displaying the Male (blue) and Female (green) total duration, rate per minute and number of visits across the 12 films in temporal order. The total area of the two colours appears to be much the same but there is no systematic difference between adjacent columns. This is possibly because equality of investment is distributed across time rather than at each visit.

Secondary analyses

On average barn swallows fledge at day 21 (Turner, 2006). Seven days of filming therefore represents a significant portion of chick development and parental investment. Given this, a secondary concern was to track any changes in investment over time. An ordinal variable, Day, was created that simply grouped film subsamples into days 1 to 7 (see Table 2 above). A bivariate Spearman's correlation was conducted between Day and the three behavioural categories, collapsed across Sex as equality of investment had been established. The results for duration ($r=-0.384$, $p=0.01$), rate per minute ($r=-0.324$, $p=0.027$) and number ($r=-0.335$, $p=0.023$) were all significant as one tailed tests and demonstrated a negative relationship with Day such that as time passed investment, as measured by these three variables, reduced. Figure 3 displays scatterplots with fitted regression lines for all of these relationships, as well as the R^2 estimates for the linear relationships. These relationships accounted for approximately 19% (duration), 12% (rate per minute) and 12% (number) of the variance in the investment variables.

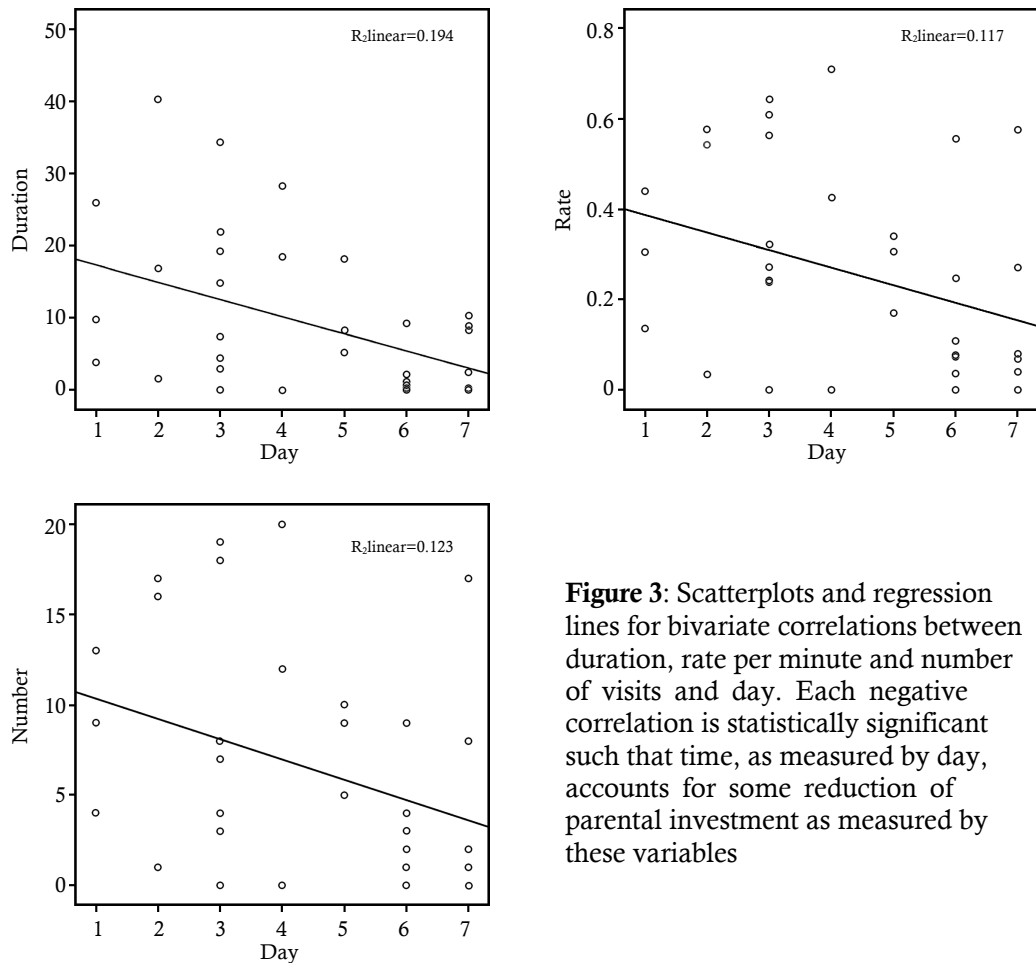


Figure 3: Scatterplots and regression lines for bivariate correlations between duration, rate per minute and number of visits and day. Each negative correlation is statistically significant such that time, as measured by day, accounts for some reduction of parental investment as measured by these variables

Time of day may have influenced investment also. From Table 2 above it can be seen that four of the films were recorded during the morning and the remaining eight during the afternoon across the seven days. Given this uneven distribution a non-parametric Mann-Whitney test was conducted to investigate differences in all three behavioural categories across the morning and afternoon. The results for duration ($U=1.176$, $p=0.251$), rate per minute ($U=1.311$, $p=0.190$) and number ($U=1.129$, $p=0.265$) were all non-significant, indicating that there was no difference in investment as a consequence of time of day.

Tertiary analysis

Whilst investment appears at equality, and evenly distributed across the day, this does not mean that adults are engaged in precise turn taking. In order to address this a two-step lag sequential analysis was conducted using Observer XT version 11. This analysis calculated the probability that either a Male or Female Present followed an initial behaviour of either Male or Female Present. The results indicated that if the Male were present then there was a 43% probability that the Male would again be present at the next visit, a 45% probability that the Female would be present at the next visit, and

a 7% probability that an Unknown would be present at the next visit. However, if the Female were present then there was a 50% probability that the Male would be present at the next visit, a 37% probability that the Female would again be present at the next visit, and an 8% probability that an Unknown would be present at the next visit. See Figure 4 for a graphical summary.

It should be noted that the Unknown category was necessarily entered into this analysis because of the way in which the coding was done. If an Unknown were present then there was a 28% probability of the Male being present at the next visit, a 44% probability of the Female being present at the next visit, and a 6% probability of an Unknown being present at the next visit.

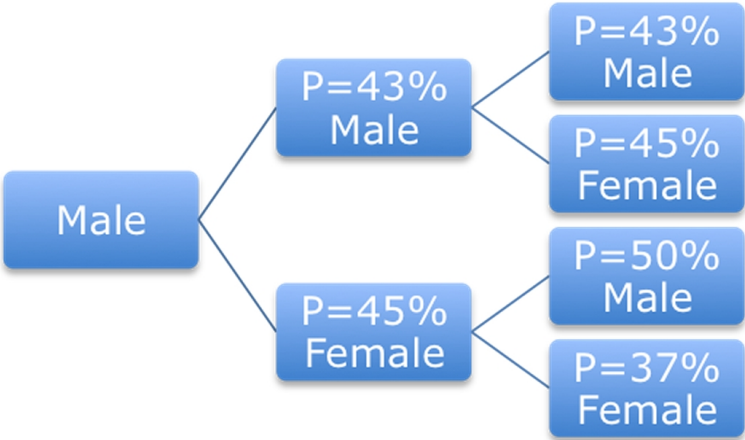


Figure 4a: A representation of possible behavioural sequences starting with an initial Male Present on the left of the diagram. Following this behaviour the probability (P) of another Male Present is 43% and of a Female Present is 45%, as depicted in the second column. The third column represents the next set of likelihoods

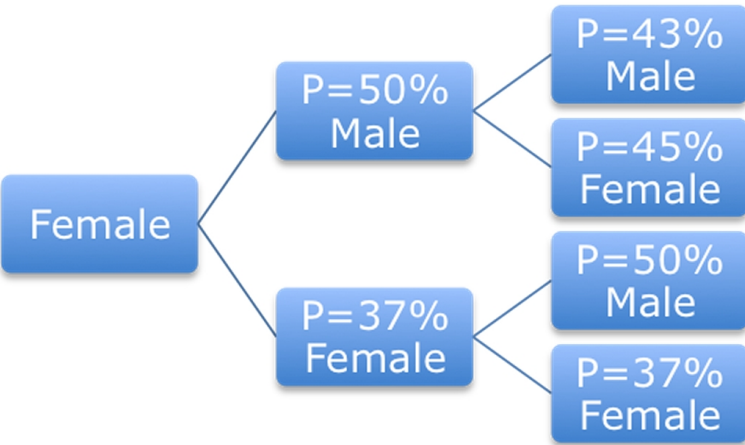


Figure 4b: A representation of possible behavioural sequences starting with an initial Female Present on the left of the diagram. Following this behaviour the probability (P) of another Male Present is 50% and of a Female Present is 37%, as depicted in the second column. The third column represents the next set of likelihoods

These probability estimates do not add up to 100% because of the nature of the film sample. At some point the film stops after a final Absent coding under a Sex category. The two-step lag sequential analysis will effectively note the preceding Present and then no following legitimate behavioural category, which would be another Present under a Sex category. Similarly the first Present coded under a Sex category has no available antecedent data point, due to the finite sampling procedure.

Given the presence of the Unknown this analysis is difficult to interpret but it appears that Male and Female sequences of attendance are close to chance suggesting that neither one of the adults is specializing in foraging at more distant sites, or upon more difficult to capture prey relative to one another. However, without more data this cannot be moved beyond speculation.

DISCUSSION AND FUTURE DIRECTIONS

The results for the focal nest reveal that the adult swallows were investing equally in the duration, rate-per-minute and number of visits to the nest, which supports the main hypothesis for this study. Moreover, these measures of investment marginally declined across a seven-day period. This should not be taken as indicative of a reduction in what might be termed true investment. Chick development will bring different requirements over time and it is possible that the adults were bringing higher value food items to the nest on later visits as chicks became able to process them. Finally, it would appear that the adults are close to chance in the sequence of their visits to the nest, in other words there was no precise turn taking in terms of care.

As a focal nest study the results in this paper should not be unjustifiably generalized but rather regarded as indicative and requiring further pursuit. One of the reasons for pursuing this study was to stimulate further work on the Lundy swallows. Given the small number of nesting pairs on the island it may be possible to record behaviour for the entire colony across a breeding season. However, this would depend upon the site of the nest. The focal nest used in this study was readily observable with minimal disturbance to the swallows and the residents of Old House North. With increased technological sophistication small cameras could be mounted near to nests prior to the return of breeding swallows and operated remotely. This would yield valuable data, including better capability to record chick behaviour and any possible differential investment across chicks.

In order to fully understand the dynamics of the breeding population on Lundy many questions require answering. To be sure of extra-pair activity DNA analyses would be required to calculate relatedness within and between nests. In the introduction reference was made to the availability of prey throughout the breeding season. A survey of variety and number of flying insects and hunting grounds across the season would be informative, as would tracking of swallow attendance in particular parts of the island across time.

The position of Lundy, as an Atlantic island, makes it vulnerable to high winds and significant aerodynamic challenges. One of the costs to males with long tails is a reduction in aerial/flying ability, and they tend to only catch smaller prey items. Indeed, male tail-length is geographically distributed such that it is much closer to the optimal value for hunting in lower latitudes with less sexual selection for that trait (Turner,

2006). It is possible that the males who breed on Lundy have shorter tails than the mean of those found elsewhere on the mainland United Kingdom, enabling them to deal with the particular aerial challenges of island life and possibly a different array of available insects. Thus, the breeding males on Lundy might be regarded as relatively low quality compared with mainland swallows in Devon, for example, yet better adapted for island life. Following from this we might expect female choice to be driven more by other characteristics such as the size of tail spots and feather condition.

In conclusion, parental investment at all nest sites on Lundy would bear scrutiny in order to further test the hypothesis that adult males and females invest equally in their chicks. In this way we can seek to reduce the variance in the existing dataset and have more certainty of core behavioural patterns. DNA analyses of relatedness would further enhance our understanding of the reproductive strategies at work on the island, and all of this data needs contextualizing with relevant ecological variables. If Lundy proves to be low on extra-pair reproductive competition it would make the island an excellent baseline site for continued study of the life histories of these birds.

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